

THE STRUCTURE, EVOLUTION AND
NOMENCLATURE OF THE OSTRACOD HINGE

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THE STRUCTURE, EVOLUTION AND NOMENCLATURE OF THE OSTRACOD HINGE

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SYNOPSIS

A revision of Middle Jurassic ostracods from the Fullers' Earth Clay has revealed a series of hinge-types which clearly demonstrate transitional stages between those commonly known as merodont and those known as amphidont. Their study has justified the classification of hinge-types according to the stage reached in a morphogenetic series. The primitive hinge is tripartite in character, and more specialized hinge-types originate by the subdivision of the median element of the basic three. The morphology of the ostracod hinge is discussed, a rational classification is proposed, and in the light of this classification, the terminology of both the hinge as a whole and that of its constituent parts is reviewed. The evolution of the post-Palaeozoic Cytheracea is traced from Palaeozoic ancestors with a similar hinge but different muscle-scar pattern, and a new superfamily, the Quasillitacea, is proposed for these Palaeozoic forms. Two new genera are proposed, *Acanthocythere* (Middle Jurassic) and *Dictyocythere* (Upper Jurassic). The latter is divided into two subgenera, *Dictyocythere* sensu stricto and *Rhysocythere* nov. The distribution of the species of *Dictyocythere* in the Upper Jurassic of England and northwest Germany suggests that the "Purbeck" Beds of the Aylesbury and Swindon districts are earlier than Middle Purbeckian, and that the "Wealden 2" of the German sequence is probably equivalent to the upper part of the Middle Purbeck Beds of Dorset. The development of the hinge in *Dictyocythere* is shown to be palingnetic.

I. TERMINOLOGY OF THE OSTRACOD HINGE

THE hinge structures of fossil ostracods play an important part in their taxonomic determination, but unfortunately the terms used for their description are ambiguous. Thus the terms "taxodont" and "heterodont" have been used to describe the compound hinge of ostracoda, not always with quite the same meaning. As used by Bold (1946), Kingma (1948), Grekoff (1952) and Malkin (1953),¹ "taxodont" refers to the presence of denticulate elements, and "heterodont" to the development of high, pointed teeth and a hinge-bar. The terms (which have been borrowed from those used to describe the lamellibranch hinge) are not altogether appropriate in their new context, and seem likely to lead to ambiguity. The term "taxodont" as used in lamellibranchs refers to the occurrence of an alternate tooth and socket arrangement, essentially similar in both valves. An exactly similar structure is not known to occur in the Ostracoda, although an alternate tooth and socket arrangement (here termed "interdentate") is not infrequently found in some or all of the elements

¹ Malkin (1953) also defines the terms adont, dysodont, desmodont, crasidont and archidont. These terms are not referred to further in this paper, as they do not describe hinge structures here dealt with.

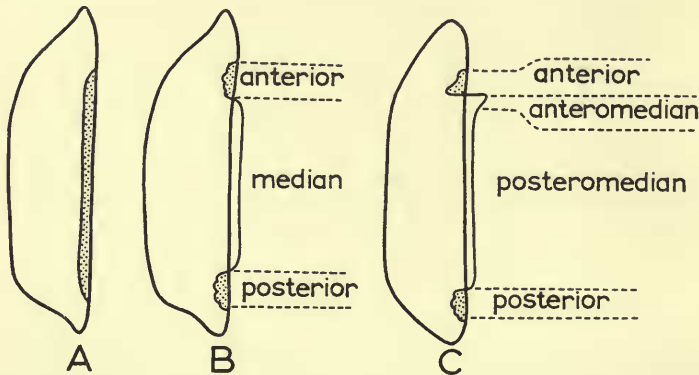
of the compound hinge. This arrangement might well be called "taxodont" and the term has in fact been so used by Kesling (1951); this use of the term is not, however, equivalent to that of the earlier definitions, and it would seem advisable to abandon it to prevent further confusion.

Other authors have used different terms descriptive of the same structures; thus "merodont" = "taxodont", and "amphidont" = "heterodont" (e.g. Triebel 1950; Pokorny, 1952). These terms are not open to the same objections, and are adopted here and fully defined below. Additional terms are also introduced; some of these are new, some are after Triebel. Technical terms, in standard English, or anglicized from Latin roots, are used to designate structures of the individual elements; terms derived from the Greek and terminating in "-dont" are used to designate the hinge structure as a whole.

2. DEFINITIONS OF HINGE ELEMENTS

The hinge structure of the ostracod carapace may be *simple* or *compound*.

The *simple hinge* ("adont" of Grekoff, Bold and Kingma) may be thought of as made up of a single *element*, which consists of a groove along the margin into which fits the edge of the other valve (Text-fig. 1, A). The hinge is not further differentiated.



TEXT-FIG. 1.—Diagrams of left valves of three ostracods, dorsal view, to illustrate division of hinge into "elements". (Stippled areas represent sockets).

The *compound hinge* is divided into three or four elements in each valve. Primarily there are three elements, anterior, median and posterior (Text-fig. 1, B). Usually these elements alternate so that if (as is usual in the right valve) the anterior and posterior are ridges, the median element separating them will be a groove; or if (as is usual in the left valve) the terminal elements are grooves or sockets, the median will be a ridge. Though genera are known which are exceptions to this (in *Haplocytheridea*, for example, all three elements of the left valve are grooves, those of the right being ridges), the distinction between the constituent elements remains clear, the terminal elements being more coarsely dentate than the median.

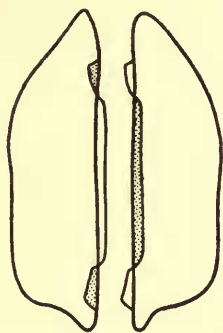
It will be shown below that the more primitive compound hinge with three elements

evolves, by subdivision of the median element, into a more advanced type in which there are four elements—anterior, anteromedian, posteromedian and posterior. The division into two parts of the median element is at first not pronounced—the anterior part being merely more coarsely dentate than the posterior (Text-fig. 2, c), but later developed forms have a more clear-cut distinction, the anteromedian becoming rather similar in proportions to the anterior element, the posteromedian usually being much the longest element of the four (Text-fig. 1, c). Rarely the anterior element also becomes differentiated, with denticles of two sizes (e.g. *Amphicythere* and *Dictyocythere*; see p. 14).

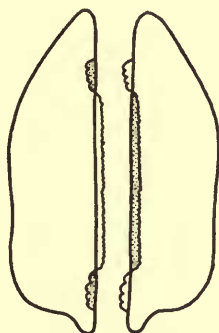
These hinge elements themselves display a great deal of variation, and the following definitions are of terms used in their description :

A. *Ridge and groove.*

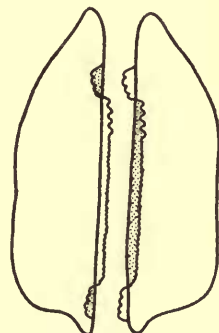
1. A hinge element may consist of a smooth *ridge* fitting into a corresponding *groove* in the opposite valve, e.g. the median element of *Camptocythere* (Text-fig. 2, A).



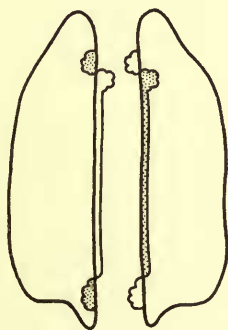
A. Lophodont



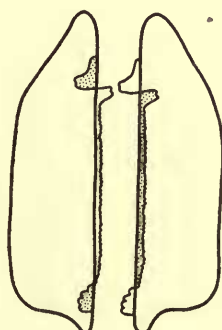
B. Merodont



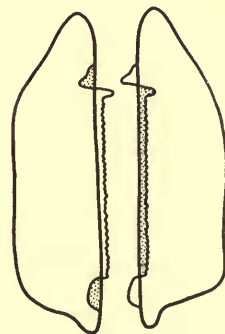
C. Entomodont



D. Lobodont



E. Schizodont



F. Amphidont

TEXT-FIG. 2. Diagrams illustrating the six main types of dentition developed in the ostracod hinge. Each pair of valves in dorsal view. (Stippled areas represent sockets).

2. A *dentate* element consists of a ridge divided into projections (*denticles*) which fit into a socketed groove termed *loculate*.
3. The median element may be furnished with finer denticles, when it is termed *denticulate*, the groove *locellate* (Text-fig. 2, B).
4. A ridge may be divided into separate teeth between which lie alternating sockets for the reception of projections from the complementary groove. Such a ridge is termed *interdentate*, the groove *interloculate*.
5. The median element of the left valve (which is usually a ridge or a bar) often lies under an elongated, sub-triangular, excavated area termed the *accommodation groove*. This, it would seem, serves to receive the projecting dorsal edge of the right valve when the carapace is open.

B. Bar.

6. The median element may consist of a ridge which is raised up from the shell margin behind it ; this is differentiated as a *hinge-bar*.

C. Boss and pit.

7. An element may be raised up as a hemispherical *boss*, which may show division into two or more lobes, when it is referred to as *bi-*, *tri-*, or *multi-lobate* ; a lobate boss fits into a *loculate pit* in the complementary valve (Text-fig. 2, D).

D. Tooth and socket.

8. An element may consist of a single tooth, projecting from a platform which itself projects more or less beyond the hinge margin, when it is referred to as *stirpate* (e.g. the anterior element in *Trachyleberis*) (Text-fig. 2, F).
9. The tooth may be a simple, more or less *conical* projection ;
10. or it may have more or less parallel sides, when it is called *pegsular* ;
11. or it may be split into two lobes, when it may be called *bifid* (Text-fig. 2, E) ;
12. or it may be *crescentic*, half-surrounding a socket ;
13. or it may be a slightly elongated and slightly curved projection, when it is termed *reniform* (as in the posterior element of many amphidont hinges (Text-fig. 2, F). A reniform tooth may be smooth (*Hemicythere* or *Trachyleberis*) or lobate (*Bradleya*) or dentate (some species of *Cythereis*).

3. CLASSIFICATION OF HINGE TYPES

Using the above definitions of the elements of the compound hinge as a basis, it is possible to classify hinges developed in the Cytheracea in the six main groups outlined below. This classification does not take into consideration hinge-types developed in other superfamilies of the Podocopa. For example, whereas the Quasillitacea (here defined) have hinges very like the Cytheracea (though apparently confined to the more primitive lophodont and merodont types), the Bairdiacea have a more complicated compound hinge not always homologous with that in the Cytheracea—compare, for example, *Bairdoppilata* (Coryell, Sample & Jennings, 1935) with *Macrocypris* (Sylvester-Bradley, 1948c) and *Triebelina* (lophodont ; Triebel, 1948). The Cypridacea,

on the other hand, have mostly simple hinges with a single element, though a few are lophodont (e.g. *Cypridea*; Sylvester-Bradley, 1949).

1. **Lophodont:** e.g. *Bythocythere*, *Camptocythere*, in which the hinge elements are divided into three in each valve, all consisting of ridges and grooves (Text-fig. 2, A). The most usual arrangement is as follows:

	Left valve	Right valve
<i>Anterior element</i> . .	Groove	Ridge.
<i>Median element</i> . .	Ridge	Groove.
<i>Posterior element</i> . .	Groove	Ridge.

2. **Merodont:** (= "taxodont" of some authors) e.g. *Cythere*, in which anterior and posterior elements are dentate or loculate, the median element either smooth or denticulate, but not subdivided (Text-fig. 2, B). The most usual arrangement is as follows:

	Left valve	Right valve
<i>Anterior element</i> . .	Loculate groove	Dentate ridge.
<i>Median element</i> . .	Denticulate ridge	Locellate groove.
<i>Posterior element</i> . .	Loculate groove	Dentate ridge.

The elements in some merodont genera (e.g. the terminal elements of *Pleurocythere*) are interdentate and interloculate rather than dentate and loculate. Many species of Middle Jurassic age have a merodont hinge with smooth median element (e.g. *Schuleridea*), and this condition may well be the more primitive.

3. **Entomodont:** e.g. *Lophocythere*, *Progonocythere* and *Xenocythere* (Triebel, 1949, 1951), in which the median element becomes subdivided, the anterior part remaining dentate, the posterior smooth or denticulate (Text-fig. 2, c). A common arrangement is as follows:

	Left valve	Right valve
<i>Anterior element</i> . .	Loculate groove	Dentate ridge.
<i>Anteromedian element</i> . .	Short dentate ridge	Short, wide loculate groove.
<i>Posteromedian element</i> . .	Long denticulate ridge	Long, narrow locellate groove.
<i>Posterior element</i> . .	Loculate groove	Dentate ridge.

The genus *Macrodentina* has a hinge transitional between entomodont and lobodont (see p. 14).

4. **Lobodont:** e.g. *Acanthocythere* gen. nov., in which the anterior element and the anteromedian elements are lobed bosses (see Pl. 1, figs. 3, 4, 8, 9; Text-fig. 2, D).

	Left valve	Right valve
<i>Anterior element</i> . .	Loculate pit	Lobate boss.
<i>Anteromedian element</i> . .	Lobate boss	Loculate pit.
<i>Posteromedian element</i> . .	Smooth or denticulate bar	Smooth or locellate groove.
<i>Posterior element</i> . .	Loculate groove	Dentate ridge.

The genus *Amphicythere* has a dentition transitional between lobodont and amphidont. The anterior element is lobate, but the antero-median element is almost entire (see p. 14).

5. **Schizodont:** e.g. *Schizocythere*, *Palmenella*, *Paijenborchella* (Triebel, 1950), in which teeth of the anterior and anteromedian elements are bifid (Text-fig. 2, E).

	Left valve	Right valve
<i>Anterior element</i> . . .	Biloculate socket	. Bifid, stirpate tooth.
<i>Anteromedian element</i> . . .	Bifid tooth	. Biloculate socket.
<i>Posteromedian element</i> . . .	Denticulate bar	. Locellate groove.
<i>Posterior element</i> . . .	Loculate socket	. Lobate, reniform tooth.

6. **Amphidont:** (= "heterodont" of some authors; Triebel uses the term amphidont in a wider sense than that proposed here—to include dentitions of both schizodont and lobodont types) e.g. *Dictyocythere*, *Trachyleberis*, in which the median element is further differentiated into a single anterior tooth and a posterior bar or ridge. A common arrangement (Text-fig. 2, F) is as follows:

	Left valve	Right valve
<i>Anterior element</i> . . .	Socket	. Stirpate tooth.
<i>Anteromedian element</i> . . .	Conical or pessular tooth	. Socket.
<i>Posteromedian element</i> . . .	Smooth or denticulate bar	. Smooth or locellate groove.
<i>Posterior element</i> . . .	Loculate socket	. Lobate, reniform tooth.

Young moults of amphidont species usually have merodont or entomodont hinges (see p. 19). The ontogeny is therefore recapitulatory.

This classification is not comprehensive. The hinge structures listed form a useful morphogenetic series, but complications are developed in some genera which are not covered—for example, the differentiations of the median element found in some genera of the Cytherideinae (e.g. *Cytheridea*, *Cyprideis*), and the development of crescentic teeth in the terminal elements in *Loxoconcha* and other genera.

4. THE EVOLUTION OF THE HINGE AND ITS BEARING ON THE CLASSIFICATION OF THE PODOCOPIA

Well-defined compound hinge-structures are particularly characteristic of the superfamily Cytheracea, which in post-Palaeozoic times provided a far greater number of species of marine ostracods than all the remaining superfamilies taken together. The series of hinge-types classified above is a morphogenetic series and not phylogenetic. Genera have passed through the various stages at different times during their racial history. The most advanced stage reached by Middle Jurassic times is the lobodont, but the amphidont hinge appears before the close of the Upper Jurassic (e.g. *Dictyocythere*, see p. 14). It is not unlikely that earlier genera with an amphidont hinge remain to be discovered. In Recent and Tertiary ostracods, merodont and amphidont hinge-structures predominate but entomodont hinges also occur (e.g. *Leptocythere*); in Middle Jurassic times the Cytheracea have hinges which are pre-

dominantly either merodont (usually with a smooth median element) or entomodont ; lobodont hinges are rare. Elsewhere (Sylvester-Bradley, 1948b) attention has been drawn to the series leading from the Middle Jurassic *Oligocythereis* (entomodont) through the Cretaceous *Cythereis* to the Tertiary and Recent *Trachyleberis* (amphidont). This series is thought to be broadly phylogenetic, and the three genera in question are placed in the same subfamily, the Trachyleberidinae. Several other undescribed genera from the Middle Jurassic have reached various stages in similar series. It seems unlikely that any of these forms are directly related to the Trachyleberidinae ; they probably represent other lineages undergoing parallel evolution. The acquisition of the amphidont hinge is considered to be a well-marked trend. If this view is correct, the diagnosis of the subfamily Progonocytherinae (Sylvester-Bradley, 1948a : 189) for Cytheracea with entomodont hinge, needs drastic revision, and it is now suggested that *Lophocythere*, *Progonocythere* and *Oligocythereis* should not be grouped together in one subfamily, although they all have entomodont hinges.

Before attempting to assess which of the hinge-types described can truly be taken as primitive, it is necessary to refer to older faunas and seek possible Palaeozoic ancestors of the Cytheracea.

The genus *Monoceratina* is the longest lived of the Cytheracea according to present ideas. The type species is Carboniferous in age, and Recent species have been recorded (Stephenson, 1946 ; Bold, 1946). However, the hinge structure is rather obscure ; the shape differs much from the majority of the Cytheracea ; the muscle-scar patterns differ sufficiently in different species to warrant query as to whether there has not been a mistake in the identification of some of the post-Palaeozoic material, and it is not in any case easy to postulate that *Monoceratina* exhibits an ancestral type of hinge-structure.

Perhaps the Palaeozoic family that most invites comparison with the Cytheracea is the Middle Devonian Ropolenellidae first described by Coryell & Malkin (1936), especially the two genera *Ropolenellus* and *Euglyphella*. By the courtesy of Mr. Raymond R. Hibbard, who presented me with several samples rich in ostracods, which he collected from the Middle Devonian of New York State, I am able to describe the more intimate details of the shell of some species of *Euglyphella*. Some of the earlier authors who dealt with the Ropolenellidae have oriented the ostracods so that the higher end is posterior. The investigation of the hinge reveals that they are closely analogous, if not homologous, with those found in the Cytheracea ; the higher end is therefore here regarded as anterior in conformity with the known orientation of the Cytheracea. Consequently the terms "left" and "right" used here have the reverse meaning to those used in description by some previous authors.

The shape of these two genera of the Ropolenellidae, in marked contrast to many other described species of Palaeozoic ostracods, is similar to many genera of the Cytheracea (Pl. 2, figs. 5-7). A broadly rounded anterior tapers to a narrow, rounded or triangular posterior. Either or both ends may be spinose. The hinge-line is straight, delimited by well-marked anterior and posterior cardinal angles and is shorter than the length of the shell. The ventral border is straight or slightly concave.

The genus *Euglyphella* was proposed by Warthin (1934) with *Strepula sigmoidalis* Jones as type species. Several other species have since been assigned to the genus.

It possesses a striking ornament of carinae not unlike those developed in many post-Palaeozoic Cytheracea (e.g. *Lophocythere*, from the Bathonian; see Sylvester-Bradley, 1948a). The hinge in *Euglyphella* is divided into three elements as follows:

	Left valve	Right valve
<i>Anterior</i>	Rather long, deeply overhung, loculate groove	Projecting ridge, forming a continuation of the selvage.
<i>Median</i>	Bar, lying below a long, narrow accommodation groove	Long groove.
<i>Posterior</i>	Short, curved loculate groove	Short, curved projecting ridge.

The hinge margin of this genus is in fact almost exactly similar to that of many post-Palaeozoic Cytheracea. The loculate nature of the terminal elements in the left valve cannot be made out in more than a few specimens, and I have not detected any specimen showing a corresponding dentation on the terminal elements of the right valve, but this may well be due to indifferent preservation.

The free margin is also similar to that seen in many Cytheracea. There is a wide duplicature, no vestibule, but a pronounced selvage. The muscle-scar pattern, however, is quite unlike anything known in the post-Palaeozoic Cytheracea; a central, circular muscle-scar pit bears a cluster of small oval scars in the form of slight tubercles, which are in close juxtaposition.

Another genus referred by Coryell & Malkin (1936) to the Ropolenellidae is *Bufina* (Pl. 2, figs. 3, 4). Species of this genus differ somewhat in shape from *Euglyphella* and *Ropolenellus* in that the dorsal margin of the left valve is markedly curved. The characteristic ornament of the genus is unlike that of any post-Palaeozoic ostracod known to the author, though Henningsmoen (1953) has pointed out that it is shared by other Palaeozoic genera such as *Ponderodictya* (see below). The details of hinge, duplicature and muscle-scar, however, are as described for *Euglyphella*, and though Coryell & Malkin were clearly correct in concluding that the genera are related, Henningsmoen is probably right in removing *Bufina* to the Quasillitinae.

The Ropolenellidae are apparently only known from Middle Devonian strata, in which they are often fairly common. They seem to represent a successful though short-lived line of evolution which in many respects anticipated the much later Cytheracea.

Another family well represented in the Middle Devonian of North America is the Quasillitidae. An examination of *Quasillites* (Pl. 2, figs. 1, 2) shows that it has a hinge-structure very similar to that of the Ropolenellidae and the two families should almost certainly be grouped together. Henningsmoen (1953) regarded them as subfamilies of one family; it is here suggested that they are related families in the same superfamily, the Quasillitacea (see p. 11). Near to *Quasillites* is the Carboniferous genus *Graphiadactylus*.

It may also be mentioned that the genus *Ponderodictya* (described by Coryell & Malkin from the Middle Devonian and placed by them in the Cytherellidae; see figs. in Triebel, 1954) bears a hinge comparable to that of the Ropolenellidae, differing mainly in that the anterior element is longer in proportion (as long, in fact, as the

median element). The ornament is not unlike that developed in *Bufina*. The genus has been placed in the Healdiidae as a member of the Platycopa (Henningsmoen, 1953; Triebel, 1954), but the hinge makes this assignment a little doubtful. *Ponderodictya* may perhaps be a member of the Quasillitacea, and as such one of the Podocopa. It is clear that in Devonian times the Healdiidae, Quasillitidae and Bairdiidae possessed characters in common which suggest that all three families had been derived from a common ancestor of not much greater antiquity than the Devonian. Subsequently the three families diverged in morphology so that they have been placed far apart in classification.

From the foregoing brief survey it will be seen that several families of Palaeozoic ostracods possessed features in common with the later Cytheracea. It seems probable that the first members of the Cytheracea were derived from one or more of the Quasillitacea towards the close of Palaeozoic time. Somewhat similar views have been advanced by Kellett (1943). Thus the superfamilies Quasillitacea and Cytheracea form part of the suborder Podocopa, and are distinguished by the muscle-scar pattern, which in the Quasillitacea is *aggregate* (i.e. consisting of a group of individual scars crowded in close juxtaposition; Pl. 2, figs. 3, 4, 6), and in the Cytheracea *discrete* (i.e. consisting of a series of individual scars separated from each other).

The primitive hinge was therefore lophodont. Whether the elements were primitively dentate or smooth cannot be certainly stated, for the apparently smooth elements in much Palaeozoic material may well be due to a loss of finer structure on recrystallization. The fact that loculate grooves have been detected in the terminal elements of both *Euglyphella* and *Quasillites* shows that at least the terminal elements were dentate in these genera by Devonian times. Some Palaeozoic specimens show a well-developed accommodation groove, so that structure cannot be taken as an advanced feature. It seems to be the inevitable consequence of any considerable difference in size between the two valves.

5. SYSTEMATIC DESCRIPTIONS

Suborder PODOCOPA

Superfamily QUASILLITACEA (Coryell & Malkin).

(First introduced here as a superfamily)

TYPE GENUS. *Quasillites* Coryell & Malkin. (Middle Devonian.)

DIAGNOSIS. Podocopa with a primitively tripartite hinge and an aggregate muscle-scar pattern.

FAMILIES INCLUDED. Quasillitidae (including Graphiadactyllidae) and Ropolenellidae. Other families no doubt remain to be described.

REMARKS. Distinguished from Cytheracea by muscle-scar pattern; from Cypridacea and Bairdiacea by hinge and muscle-scar pattern; from Healdiidae (Platycopa) by hinge.

DISTRIBUTION. So far known only from the Palaeozoic. Mesozoic Platycopa with an aggregate muscle-scar pattern are, however, known (*Ogmoconcha*, Lower Lias)

and it may be expected that the Podocopa underwent a parallel development; Mesozoic Quasillitacea may yet be discovered.

Superfamily CYTHERACEA

Family uncertain

Genus *ACANTHOCYTHERE* nov.

TYPE SPECIES. *Cythere sphaerulata* Jones & Sherborn, 1888: 253, pl. 1, fig. 6.

DERIVATION OF NAME. ἀκανθα, a thorn or prickle + genus *Cythere*. Gender: feminine.

DIAGNOSIS. Cytheracea with lobodont hinge, surface more or less spiny, carapace plump, eye tubercles shiny, rather prominent.

OCCURRENCE. The two species of the genus here described are so far known only from the Upper Fullers' Earth Clay (Bathonian) of the Bath district.

Acanthocythere sphaerulata (Jones & Sherborn)

(Plate 1, figs. 1-4)

1888. *Cythere sphaerulata* Jones & Sherborn, p. 253, pl. 1, fig. 6.

DIAGNOSIS. Carapace oblong, tumid, ornamented with closely-set blunt spines arranged in a faint reticulate pattern.

HOLOTYPE. Geol. Dept. Brit. Mus. (N.H.) no. I.1835. A complete carapace.

TYPE LOCALITY. "Yellow Fullers-earth Clay, Midford" (Jones & Sherborn, 1888: 254).

OTHER FIGURED SPECIMENS. Geol. Dept. Brit. Mus. (N.H.) nos. In.42433-34.

DESCRIPTION. Both valves with sub-parallel dorsal and ventral margins, no taper, anterior and posterior ends evenly rounded. Sexual dimorphism rather pronounced, the presumed males longer than females.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace ♂ (I.1835; holotype)	0.51	0.31	0.32	1.65	1	1.03
Left valve ♂ (In.42434)	0.67	0.37	0.26	1.81	1	0.70
Right valve ♂ (In.42433)	0.69	0.38	0.22	1.82	1	0.58

The whole surface (with the exception of the eye tubercles) covered with very fine spines set close together and forming a reticulate pattern which is clearer in worn specimens than in those more perfectly preserved.

Normal pore canals large, sparse, about 20 to the valve in the female. Radial pore canals simple, sparse, straight, about 8 to the anterior end. Duplicature fairly wide at anterior end (Pl. 1, fig. 3), with flange-groove well developed in left valve. Muscle-scar not seen. Hinge lobodont, in detail as follows:

Hinge element	Left valve	Right valve
<i>Anterior</i>	Circular pit, presumably loculate	4-lobate boss.
<i>Anteromedian</i>	4-lobate boss	Oval pit, presumably loculate.
<i>Posteromedian</i>	Smooth bar lying below accommodation groove which is rather wide in the female, but narrow, and developed only in posterior half in male	Narrow groove lying below rather prominent dorsal margin which forms a ridge complementary to the accommodation groove.
<i>Posterior</i>	Loculate groove	Prominent, slightly curved 5 to 7 dentate ridge, set at a slight angle to the median element.

The state of preservation is not sufficiently perfect to make it quite certain that the posteromedian element is not denticulate.

MATERIAL. Fourteen specimens (in addition to the holotype) from the same horizon and locality as *A. spiniscutulata*.

Acanthocythere spiniscutulata n. sp.

(Plate 1, figs. 5-9)

DERIVATION OF NAME. Latin *spina*, spine + *scutulatus*, diamond-shaped.

DIAGNOSIS. Carapace tapering, with prominent cardinal angles; ornament of subtriangular or diamond-shaped spinose ridges.

HOLOTYPE. Geol. Dept. Brit. Mus. (N.H.) no. In.42435. A left valve.

TYPE LOCALITY. Upper Fullers'-Earth Clay (in top foot of economic "Fullers Earth"), Fosse Way Fullers'-Earth Mine, near Bath. Nat. Grid. ref 31/727613. Author's field ref. no. 47 *FW* 9.

PARATYPES. Same locality and horizon. In.42436-37.

DESCRIPTION. Carapace tapering, in side view, towards posterior. Ornament of subtriangular or diamond-shaped rather coarsely spinose ridges. Sexual dimorphism not observed.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace (In.42437)	0.57	0.40	0.35	1.43	1	0.88
Left valve (In.42435; holotype)	0.57	0.37	0.22	1.54	1	0.59
Right valve (In.42436)	0.56	0.32	0.19	1.75	1	0.59

Details of hinge, duplicature and pore canals as in *A. sphaerulata*.

MATERIAL. Nine specimens from the type-locality and horizon.

Genus *DICTYOCY THERE* nov.

TYPE SPECIES. *Cythere retirugata* Jones, 1885: 350, pl. 9, figs. 21-24.

DERIVATION OF NAME. δίκτυον, a net + genus *Cythere*. Gender: feminine.

DIAGNOSIS. More or less trapezoidal Cytheracea, usually reticulate, with amph-

dont hinge, the anterior element undifferentiated (subgenus *Dictyocythere*) or differentiated into denticles of two sizes (subgenus *Rhysocythere*), the posterior element dentate. No accommodation groove. Eye tubercles not developed.

OCCURRENCE. This genus includes several species from the Purbeck Beds of Buckinghamshire and Swindon, the Middle Purbeck Beds of Dorset and the so-called Wealden Beds of N.W. Germany. *D. transiens* is abundant in the Upper Portland Beds of the Aylesbury district.

REMARKS. Species of this genus were placed by Martin (1940) in his genus *Macrodentina*. However, the type-species of *Macrodentina* (*M. lineata*) is Upper Oxfordian; Triebel (1954) has shown that two homeomorphs were confused by earlier authors under the name *M. lineata*, one of which (the true *M. lineata*) has an advanced type of entomodont hinge, verging on the lobodont. The Kimmeridgian genus *Amphicythere*, described by Triebel in the same paper, has an interesting hinge transitional between lobodont and amphidont. In it the anterior element of the hinge has denticles differentiated into two series. This rather rare variation is also found in *Macrodentina* and in some species of *Dictyocythere*, which suggests that the three genera may be related.¹ The hinge of *Dictyocythere* resembles that of *Amphicythere* but has moved nearer to the typical amphidont type, showing its primitive nature only in those species possessing a differentiated anterior element (subgenus *Rhysocythere*). The details of the hinge of *Amphicythere semisulcata*, derived from Triebel's (1954) description, are tabulated below for comparison with those of *Dictyocythere*.

	Left valve	Right valve
<i>Anterior part of anterior element</i> .	Loculate groove	. Low tridentate ridge.
<i>Posterior part of anterior element</i>	Loculate pit	. Trilobate boss.
<i>Anteromedian element</i> . . .	Faintly bilobate boss	. Deep pit.
<i>Posteromedian element</i> . . .	Smooth ridge	. Shallow groove.
<i>Posterior element</i>	Loculate groove	. Slightly curved, 7-dentate ridge.

SUBGENERA. The fact that two hinge-types exist in the group of species here regarded as forming *Dictyocythere* might be regarded as evidence that they should be split up into two distinct genera. In other characters, however, *D. rugulata* seems to be so close to *D. retirugata* that I prefer to separate the groups as subgenera only, as follows:

(i) Subgenus ***Dictyocythere*** *sensu stricto* (with undifferentiated anterior element to hinge):

- D. retirugata* (Jones).
- D. mediostricta* n. sp.
- D. decorata* (Anderson).

(ii) Subgenus ***Rhysocythere*** (with differentiated anterior element):

- D. rugulata* (Jones).
- D. transiens* (Jones).

¹ However, fairly prominent eye tubercles are developed in *Amphicythere*, but not in the other two genera.

STRATIGRAPHICAL VALUE. The distinction, made below, between species of the genus found in the Purbeck Beds of Buckinghamshire and in the Swindon Series on the one hand (*D. (R.) rugulata*, *D. retirugata*), and in the Middle Purbeck Beds of the Dorset coast on the other (*D. mediostricta*), lends further support to the supposition that the Swindon Series (and the Aylesbury "Purbeck" Beds) were earlier than the Middle Purbeck Beds of the Dorset coast (see Arkell & Sylvester-Bradley, 1941). It appears that no species of *Dictyocythere* or of *Cypridea* is identical in the two regions¹. It is *D. mediostricta* that is found in the so-called Wealden of N.W. Germany, not *D. retirugata*, as recorded by Martin. The abundance of *D. transiens* in undoubted Portland Beds at Aylesbury (below horizons yielding *Titanites*) shows that the genus was certainly in existence before the close of Portlandian time, and it still seems possible that Blake (1885) may have been right when he suggested that the so-called Purbeck Beds of Swindon and Aylesbury were deposited at the same time as the Portland Beds further south. *D. (R.) rugulata* and *D. retirugata* have been both recorded from the Swindon Sands and Stone (Sylvester-Bradley, 1941: 358), which has always been regarded as Portlandian.

Subgenus **DICTYOCY THERE** sensu stricto

DIAGNOSIS. *Dictyocythere* with undifferentiated anterior element to hinge.

Dictyocythere (Dictyocythere) retirugata (Jones)

(Plate 3, figs. 7-10; Pl. 4, figs. 3, 4, 11, 16, 17)

1885. *Cythere retirugata* Jones, p. 350, pl. 9, figs. 21-24 (including var. *textilis*).

[not *Macrodeniina retirugata* (Jones) Martin, 1940.]

1941. *Cythere retirugata* Jones var. *textilis* Jones: Anderson, p. 374 (part), pl. 18, fig. 3, ? fig. 2.

DIAGNOSIS. Surface reticulate. Shape trapezoidal. Median constriction absent or slight. Sexual dimorphism pronounced.

LECTOTYPE (here designated). Geol. Dept. Brit. Mus. (N.H.) no. In.48601. Figured Jones, 1885, pl. 9, fig. 23. (Jones' no. 253, 11.) A right valve ♂².

TYPE LOCALITY. "Last Portland bed", Hartwell, Bucks.

DESCRIPTION. Surface evenly reticulate except immediately above muscle scar. Shape trapezoidal, with pronounced cardinal angles. Sexual dimorphism pronounced, the presumed males proportionately longer than the females.

¹ Wolburg (1950) suggests that *Uwellia papulata* Anderson from the Swindon Series may be synonymous with *Cypridea sowerbyi* Martin from N.W. Germany, but specimens of the latter species that Dr. Wolburg kindly sent me show that this is not the case. On the other hand the specimen figured by Anderson (1941, pl. 18, fig. 2) from the Middle Purbeck of Poxwell, Dorset, does appear to have been correctly identified as *Cythere retirugata*.

² Lectotype of "*Cythere retirugata* var. *textilis* Jones" (here designated): Geol. Dept. Brit. Mus. (N.H.) no. In. 48602, figured Jones, 1885, pl. 9, fig. 24. A right valve ♀. (Jones' no. 166, 1). "Shaly beds, Barnard's Pit, Hartwell".

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Left valve ♂ (In.48609)	0.92	0.47	0.25	1.97	1	0.53
Right valve ♂ (In.48608)	0.97	0.49	0.29	1.98	1	0.59
Left valve ♀ (In.48610)	0.80	0.51	0.28	1.58	1	0.55
Right valve ♀ (In.48611)	0.84	0.51	0.24	1.66	1	0.47

Normal pore canals large ; radial pore canals sparse, straight. Muscle-scar pattern of usual Cytheracea type, with four scars in vertical superposition, and a single scar in front. Hinge amphidont (see Pl. 4. figs. 3, 4, 11, 16, 17) details as follows :

Hinge element	Left valve	Right valve
<i>Anterior</i>	Pit	Smooth protuberant boss with a slight anterior swelling, perhaps representing the relict of anterior denticulation.
<i>Anteromedian</i>	Smooth protuberant boss	Pit.
<i>Posteromedian</i>	Smooth, slightly projecting bar. No accommodation groove	Smooth groove.
<i>Posterior</i>	Loculate groove	Curved, dentate ridge.

REMARKS. Jones (1885) and Anderson (1941) regarded this species as composed of a number of varieties based on differences in the strength and complexity of the reticulate ornament. Two of these varieties are here raised to specific rank, since the different ornament is correlated with slight differences in shape and with (in one case) a difference in the hinge. Moreover there are no transitional forms, and though they occur together in the same bed at Swindon, they have a different distribution at other horizons and in other localities. I have been unable, however, to maintain a distinction between the typical *D. retirugata* and the forms referred by Jones and Anderson to var. *textilis*.

OCCURRENCE. This species is abundant in the Cythere Marl of the Swindon Series at Swindon, and occurs also at higher and lower horizons. It is found at several horizons and localities in the Purbeck Beds of Buckinghamshire.

Dictyocythere (Dictyocythere) mediostricta n.sp.

(Plate 3, figs. 2-6)

1940. *Macrodentina retirugata* (Jones): Martin, p. 330, pl. 5, figs. 74-78.

DERIVATION OF NAME. Latin *medius*, middle—*strictus*, drawn tight.

DIAGNOSIS. Large, reticulate, trapezoidal *Dictyocythere*, with a slight constriction in the mid-dorsal region.

HOLOTYPE. Geol. Dept. Brit. Mus. (N.H.) no. In.48607. A male carapace (Pl. 3, figs. 3-6).

TYPE LOCALITY. Upper part of the *Cypridea fasciculata* subzone of the Middle Purbeck Beds (shale 24 ft. above the Cinder Bed ; author's field ref. no. WT 33), Worbarrow Tout, Dorset (Nat. Grid ref. 30/869796).

PARATYPE (same locality and horizon). In.48606. A female carapace (Pl. 3, fig. 2).

DESCRIPTION. Strongly reticulate and trapezoidal, superficially much resembling *D. retirugata*, but larger, and with a constriction about the middle of the back. Sexual dimorphism marked, the females usually shorter than the specimen figured :

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace ♂ (In.48607; holotype) . . .	1.12	0.63	0.56	1.79	1	0.89
Carapace ♀ (In.48606)	1.02	0.67	0.52	1.54	1	0.78

Internal details not well displayed, owing to recrystallization of material. Hinge distinctly amphidont, however, with anteromedian boss of left valve strongly protuberant.

MATERIAL AND OCCURRENCE. This is a very abundant ostracod in the upper part of the Middle Purbeck Beds of the Dorset coast, where it is associated with species of *Cypridea*, but alternates in dominance with that genus in successive beds. Hundreds of specimens have been isolated from several horizons at Worbarrow Tout, and the species has also been found at other Dorset localities. Specimens from N.W. Germany (sent by the kindness of Dr. J. Wolburg) from Lingen (Boring No. 29 at 1195 m.) are slightly smaller, but have an almost identical ornament to that of the Dorset specimens. Wolburg (1950) classifies this horizon as "Wealden 2", and correlates it with the British Upper Purbeck. The type-locality in Dorset is in the upper part of the *C. fasciculata* subzone at the top of the Middle Purbeck.

Dictyocythere (Dictyocythere) decorata (Anderson)

(Plate 3, fig. 1)

1941. *Cythere retirugata* Jones var. *decorata* Anderson, p. 374, pl. 18, fig. 4.

DIAGNOSIS. Reticulate *Dictyocythere* with a "second order" reticulation within the main cells.

HOLOTYPE. Geol. Surv. Mus. no. 70339. Figured Anderson, 1941, pl. 18, fig. 4. A right valve.

TYPE LOCALITY. Cythere Marl, Swindon Series, Swindon. Author's field ref. no. TGA 7.

REMARKS. This is a rare species known only by three specimens from the Swindon Series (Sylvester-Bradley, 1941). The hinge appears to be exactly as in *D. retirugata*, but the shape is a little different, and the ornament more complex (see Pl. 3, fig. 1); the "second-order" reticulation noticed by Anderson is not confined, as suggested and figured by him, to the centre of the valve.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Left valve (In.48618)	0.94	0.57	0.36	1.65	1	0.63

Subgenus *RHYSOCYTHERE* nov.

TYPE-SPECIES. *Cythere retirugata* var. *rugulata* Jones, 1885.

DERIVATION OF NAME. $\rho\upsilon\sigma\acute{o}\varsigma$, wrinkled + genus *Cythere*. Gender: feminine.

DIAGNOSIS. *Dictyocythere* with anterior element of hinge differentiated so that, in the right valve, an anterior group of denticles lies in front of the usual boss.

Dictyocythere (Rhysocythere) rugulata (Jones)

(Plate 4, figs. 1, 2, 5-10, 12-15)

1885. *Cythere retirugata* var. *rugulata* Jones, p. 350, pl. 9, figs. 17-20.

1941. *Cythere retirugata* Jones var. *rugulata* Jones: Anderson, p. 373, pl. 18, fig. 1.

DIAGNOSIS. Shape trapezoidal. Surface smooth over anterodorsal region, strongly ridged along venter and anterior margin.

LECTOTYPE (here designated). Geol. Dept. Brit. Mus. (N.H.) no. In.48600. A carapace, ♀, not left valve, as stated by Jones. Figured Jones, 1885, pl. 9, fig. 17. (Jones' No. 256, 2.)

TYPE LOCALITY. Hartwell, Buckinghamshire.

DESCRIPTION. Shape trapezoidal, dorsal and ventral margins being subparallel. Moderate sexual dimorphism, males somewhat longer than females and much rarer.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace ♂ (In. 48616)	0.98	0.56	0.49	1.76	1	0.88
Left valve ♂ (In.48615)	0.97	0.57	0.28	1.70	1	0.49
Left valve ♀ (In.48604)	0.84	0.55	0.29	1.54	1	0.54
Right valve ♀ (In.48605)	0.86	0.55	0.29	1.59	1	0.54
Left valve, juv. (In.48614)	0.68	0.45	0.24	1.50	1	0.53
Right valve, juv. (In.48613)	0.67	0.41	0.20	1.61	1	0.48

Valves almost smooth over the anterodorsal region of the carapace, but minutely punctate over a small region just below and behind the centre of the carapace (Pl. 4, fig. 6). Venter and anterior border strongly ridged (Pl. 4, figs. 12-14). Normal pore canals large and obvious in translucent specimens (Pl. 4, fig. 6) though they have often been misinterpreted as pits or bosses. Radial pore canals few, straight, sparse. Anterior duplicature fairly wide, with slight vestibule. Muscle-scar pattern (Pl. 4, fig. 5) consisting of four scars in vertical superposition, with one oval scar in front of them. Hinge of adult is amphidont, the anterior element clearly differentiated into an anterior group of about four small denticles in front and to a well-marked boss behind (Pl. 4, figs. 1, 2 and 10):

Adult	Left valve	Right valve
<i>Anterior element</i>	Deep pit, with an anterior loculate groove leading out from it	Protuberant boss lying at the posterior end of a dentate ridge, the denticles decreasing in size towards the anterior.
<i>Anteromedian element</i>	Rounded boss	Deep pit.
<i>Posteromedian element</i>	Smooth bar	Shallow groove.
<i>Posterior element</i>	Loculate groove	Dentate ridge.

The hinge of juvenile moults (Pl. 4, figs. 7-9) is particularly interesting, as it is transitional between merodont and entomodont, with a subdivided, nearly smooth, median element, but dentate terminal elements. The hinge of this species is therefore palingenetic, and it seems that all investigations of the ontogeny of hinge development so far published show that recapitulation takes place.

Juvenile	Left valve	Right valve
<i>Anterior element</i> . . .	Loculate groove	Dentate ridge.
<i>Median element</i> . . .	Smooth bar, the anterior end swollen and protruding further than posterior	Groove, the anterior end more deeply excavated than posterior.
<i>Posterior element</i> . . .	Loculate groove	Dentate ridge.

Dictyocythere (Rhysocythere) transiens (Jones)

(Plate 3, figs. 11-13)

1885. *Cythere transiens* Jones, p. 349, pl. 9, figs. 13-16.

DIAGNOSIS. Small reticulate *Dictyocythere*, tapering strongly to posterior in side view; with *Rhysocythere* hinge

LECTOTYPE (here designated). Geol. Dept. Brit. Mus. (N.H.) no. In.48603. A left valve. Figured Jones, 1885, pl. 9, fig. 16. (Jones' No. 364, 2.)

TYPE LOCALITY. "Lower Purbeck, Swindon" (but see below).

DESCRIPTION. Fairly coarsely reticulate, tapering strongly to posterior in side view, sexual dimorphism not observed.

	Dimensions (mm.)			Proportions		
	L	H	W	L	H	W
Carapace (In.48617)	0.60	0.37	0.31	1.61	1	0.82

Hinge appears to be exactly as in *D. (R.) rugulata*.

OCCURRENCE. Although the type locality is at Swindon, only a few specimens have been found there by the author in the "Swindon Series", and these may have been derived from the Portlandian "Swindon Sands and Stone" below. The species is abundant at a certain horizon of the "Bugle Pit", Hartwell, within the Creamy Limestones of undoubted Portlandian age (author's field ref. no. BP 18; this is from Bed 6 of Arkell, 1947: 126). The species is characteristic, in fact, of the Upper Portlandian, and only with some doubt can its range be said to include the Lower Purbeck, despite Jones' contention. The horizon "Lower Purbeck" appears to be an inference by Jones, and was not indicated by Blake, who collected the specimens (see Jones, 1885: 328).

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